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Environmental Stability and Human Evolution

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Abstract

Based on energetic and nutritional aspects of the development of an over-proportional brain size, R. MARTIN recently put forward the theory that human evolution very likely started in the stable environment of the tropical rain forest in which human ancestors could follow a high energy feeding strategy.

We accept the latter as being essential for the development of a big brain, but question the other precondition. The tropical rain forest is very low ranking in the production of nutrient and energy rich food items. According to its general ecological structure it is highly unlikely that these conditions differ significantly from those in the past few million years. Furthermore the rain forests expanded and retracted to small refugia during the late Tertiary and the Pleistocene. So this type of environment is neither more stable nor more productive than the savanna over the course of time.

We argue that MARTIN's theory is right with respect to the nutritional demands, but the other precondition, the stable environment (of the rain forest), has to be changed according to the present ecological knowledge. We suggest that the shrinkage of the tropical rain forest provided the initial external force which "pushed" the early hominids out of the forest into the open savanna, where they could avoid the competition with the more specialized apes and gain the foodstuff necessary for the promotion of the brain development.

1. Martin's theory

In a highly stimulating analysis Prof. Robert Martin from the University College of London recently* put forward the theory, that human evolution, which is closely linked to the evolution of an exceptionally big brain, should have started in a stable environment. Whatever a "stable environment" might mean, remains open, but it is clear that there is no other choice than the tropical rain forest (LEWIN 1982). He states that his "analysis demands a stable environment and high energy feeding strategy for human ancestors, going right back to the split between humans and apes some 5 million years ago. This ... is ad odds with the simple savanna hypothesis that envisages a shift to the savanna as an important stage in human evolution" (LEWIN 1982). Besides brain size and the environmental determinants for its evolution also the fact that human reproduction follows

* At the occasion of the 52nd annual JAMES ARTHUR lecture at the American Museum of Natural History, New York 1982.

the most extreme K-directed strategy among all mammals (cf. also LOVEJOY 1981), the development of which is only possible, so MARTIN's argument, in a K-selective environment, that is, a stable environment! The costly development of an oversized brain additionally demands for a high energy feeding strategy. This conclusion is drawn from extensive studies on the interrelation between relative brain weight and type of food. Insect feeders and folivorous primates produce the relatively smaller brains compared to fruit and root feeders. So "there is a good deal of evidence that might link the mother's metabolism with the developing brain of the fetus" (MARTIN after LEWIN 1982). Though MARTIN hesitates a bit to conclude strictly that rain forests must have been the proper environment for the initiation of the special brain development, he obviously sees no other possibility, because in his opinion the savanna would not provide those necessary preconditions. Whether this holds true may be questioned according to our current knowledge of the tropical rain forest environment.

2. Hold the preconditions true ?

2.1 Stability

Understanding "stability" as a low rate of change of the environment, the tropical rain forest appears to be the most "stable" ecosystem on land, though this may be only the by-product of the high diversity, which diminishes the effects of single species dynamics in a species-rich system. But even if we assume a greater stability of the tropical rain forest in the situation of the present, there can be no doubt that on an evolutionary scale of time the turnover rates equal those of other major biota of the world. Extensive reductions in size occurred several times during the Pleistocene and most probably also during the late Tertiary. Forests were reduced to more or less tiny refugia in Africa and South America (HAFFER 1979, MOREAU 1966, with more detailed references). These events overlap quite completely with the whole span of evolutionary time which gave rise to the human branch within the primates. For the time scale of the past five million years or so, we cannot assume a higher degree of persistence ("stability") for the tropical rain forests than for the savannas or any other more seasonal type of environment.

2.2 Productivity

The second argument is based on an uninterrupted high flux of energy-rich nutrients from the producer to the consumer level, i. e. from the environment to the developing hominids. With respect to this precondition, which may be in fact very essential for the development of the special brain, the argument of a tropical rain forest environment being the main ecological space in which the process could begin and proceed long enough is even more questionable. For it is a common feature of these forests now to provide less food for man than nearly any other kind of terrestrial environment.

In the tropical rain forest areas still today the density of the human population remains low or very low, despite the enormous influx of power-generating energy and additional food from extra-tropical regions. Much of the energy has to be used for transport of food and for cooling. Higher levels of local production are restricted to naturally subsidized solar-powered ecosystems (ODUM 1975) with an annual energy flow of some 20000 kilo-

calories per square meter, e. g. tidal estuaries, and riverine environments, which receive regular supply of nutrients from an extensive catchment area. But besides these exceptional situations the true rain forest environments remain poor in productivity and may have been invaded by the recent rain forest tribes under the competitive pressure of the superior tribes from outside the forests. Their culture and capabilities seem to be in a process of reduction, but are not reflecting the "primitive" (i. e. original) way of life of early human beings. With respect to rain forest productivity we have no reason to assume a higher level a couple of million years ago.

This is reflected by the density of larger mammals and higher primates in the tropical lowland rainforests too. Under natural conditions their biomass remains so low, that it differs several orders of magnitude from that of the savanna. This is surprising at least with respect to the foliage feeding monkeys and apes, which should have an abundant supply of food. But it is a most diversified supply with a low predictability where to find the next suitable food patch when one is exploited! So overall density falls well below one per cent in terms of biomass for the relation between primate foliage feeders and the standing crop. The occurrence of fruit trees is even more erratic and perhaps best exploited by flying mammals (fruit bats) and birds, for which the searching expenditure is much lower than heavier primate's walking and/or climbing. The low seasonality of the climate brings up only a limited degree of synchronization and also reduces the amount of tuber-producing plants in the understory, because there are no seasons where dormancy would be necessary.

So it is not surprising that the density of bigger mammals in the rain forests differ from that in the tropical savannas by at least two orders of magnitude. Remarkably by far the highest biomass density of bigger mammals per unit of area is found in the afrotropical savannas, which must have played an important role in the evolution of Man. This is in contrast to the savannas adjoining the largest area of tropical rain forest, the Amazonian forests, in which only a small array of medium sized primates is found. Amazonia did not give rise to any comparable development of species which could be taken as ecological equivalents to the apes.

The studies of Fittkau (1974) and Fleming (1979) demonstrate the differences in animal biomass in the different kinds of tropical forests and the geochemical situation quite extensively.

From an economic point of view one can even consider the wet tropics as being ecologically handicapped (Weischet 1980). So it is far from conclusive that tropical rain forests provided sufficient supply of proper foodstuff for a special brain development which is dependent on a high quality and quantity of nutrients. Rain forests cannot have been "paradisiac" environments for (early) humans (cf. Meggers 1971 and Meggers et al. 1973).

3. Discussion

Both preconditions considered essential by Martin are not well proven for the tropical rain forest obviously. In fact the present ecological evidence indicates the opposite. There is neither a long-lasting stability nor a productivity high enough to allow the development of an extraordinary big brain **before** the hominids made the change (or were forced to change) from the forest to the savanna. The contrary seems more likely.

But does that mean a serious critique of the brain development hypothesis? Before discussing this question, we have to consider another precondition not mentioned explicitely by LEWIN (1982) in his brief presentation of Prof. MARTIN's new hypothesis. It is the environmental force which should have exerted the selective pressure. Such a pressure is inevitably necessary for any selective process which leads to significant changes. For why should a primate living in a tropical rain forest on resources good enough to allow an intrauterine brain increase to a size which surpasses that of the bigger apes change that smooth way of living, if there are no obvious reasons? What could be the advantage of a (costly) bigger brain in the rain forest environment? Could such an evolutionary scenario work without a strong selective pressure? Adaptation is change and must be caused by changes. Stability does not permit major changes, but may complete an evolutionary fine-tuning at most.

If the quantity and quality of the food of the mothers bearing infants really is critical for the development of the big brain, then competition for food resources in short supply should exert the most powerful selective force. We may assume that human ancestors started their special evolutionary path from an intermediate size, and that they have been more generalized with respect to diet than the bigger apes which specialized to folivory. They gained a metabolic rise in the efficiency of food utilization (a food low in content of effective nutrients!) by the mere effect of size (MARTIN according to LEWIN 1982). Their average velocity of movements remains low in contrast to the smaller primates with which they inhabit the forests in partly or mostly separated feeding niches sympatric or even syntopic in places.

What could have been the effect of the shrinkage of the tropical rain forests in the late Tertiary or early Pleistocene on this array of sympatric species? Might it be possible, that the less precisely adapted "generalistic" species had been outcompeted by the specialists, when the series of close competitors was tightened? Under the strong and increasing selective pressure of a dwindling habitat full of better competitors two possibilities remain: the inferior species vanishes or it changes its habitat (at least its center of activity) into an environment, where few or no such competitors occur. That situation was certainly provided by the increasing savanna, when the forests decreased.

The expanding savanna promoted the production of fruits, root tubers (rich in starch and protein) and animal meat – exactly that kinds of food which are considered essential for the brain development (LEWIN 1982)! But these food items can be found only in a coarse grained manner and with the investment of significant amounts of searching time and exposure to danger.

So every step in the increase of the brain capacity could receive an adaptational reinforcement in the open savanna because of the new tasks which arose with the life there. Bipedal movement had to be evolved continuously to high-speed running (LOVEJOY 1981 and others) of sufficient duration (contrasting to sudden but short bursts of activity in the great apes); and the same applies to the "handling" of objects of different shapes and sizes compared to the much more uniform items in the forest (branches, twigs, and leaves or fruits), or the formation of well structured, cooperative groups. These and other aspects of human capabilities have been studied elsewhere and extensively considered in the anthropological literature. Altogether they give immediate reward for the individuals in a positive feedback system, when the brain capacity was increased. Selection could act, the-

refore, very direct and efficient on the individual level within small groups, which must have triggered the process quite extensively.

We conclude for that reasons, that the outstanding importance of the nutritional state of the baby-bearing mother is wholly compatible with the widely accepted savanna-origin of human evolution. But in our opinion it is not the persistence and stability of the jungle, which gives the clue, but its **instability in size** over the span of the past five million years. Using a logarithmic time scale one can hardly fail to see the general tendency of mankind to spread from the tropics to the subtropical and then to the temperate and even subarctic regions of the world. Each new "wave" of ecological "invasions" into higher latitudinal areas was followed up by an increase, or even a multiplying, of the numbers of humans. So the general line of adaptation leads from the edge of the forest (ODUM 1975) to the open and from the tropical to the cooler climates with their much higher productivity of harvestable food.

But the most basic step in the general development should have been the habitat change from the edge of the forest into the savanna where the hominids developed most of the biologically important morphological and physiological adaptations (e. g. bipedal movement, lunar periodizity of the female ovulation cycles, reduction of hair cover on the body to enhance the cooling efficiency of sweating – which operates hardly noticeable in the high humidity of the tropical rain forest air!), and among many others last not least the specialization onto a non-specialized way of living.

This scenario provides both, the causing force (shrinking forests) and the proximate factor (nutritional improvement), for the explanation of the basic lines of the whole process. It also offers a clue to the astonishing differences in the evolutionary processes in Africa and South America, both parts of the former Gondwana continent and the home of a different but generally comparable (MOYNIHAN 1976) primate fauna. But whereas South America lacks any development of further advanced primates and gave rise only to nothing more than a couple of medium sized monkeys quite low in brain development and "intelligence", Africa, the savanna continent, most probably gave rise to the ascent of Man.

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